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FUNCTIONAL MORPHOLOGY AND SPECIES CHARACTERISTICS OF A LARGE, SOLITARY RADIOLARIAN *PHYSEMATIUM MUELLERI*

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ABSTRACT

Physematium spp. and related genera of radiolaria (*e.g., Thalassolampe* and *Actissa*) are characterized by a large, limpid spherical cell body varying in cytoplasmic compactness, but characteristically possessing numerous small (*ca.* 3 μm dia.) symbionts held in fine radiating axopodia surrounding the large central capsulum. An analysis of the cytoplasmic organization of *Physematium muelleri* suggests that this organism has adapted to a pelagic existence by increasing surface area to enhance prey capture while conserving biomass through the development of a large internally alveolate, spheroidal cell possessing fluid-filled spaces. The thin capsular wall is supported by a network of cytoplasmic strands emanating from the perinuclear region of the intracapsulum. The fine structural organization of the cytoplasm, composition and thickness of the central capsular wall, and the amount and kind of material deposited within the perinuclear envelope appear to be more significant taxonomic discriminating characteristics than the number or kind of siliceous spicules produced surrounding the central capsulum. The possible phylogenetic relationships among some genera related to *Physematium* and the functional morphology of the large, fluid-filled central capsule of close relatives are presented.

INTRODUCTION

Radiolaria are among the most abundant of biomineralizing Sarcodina occurring widely in the world's oceans. Their diverse and elegant siliceous skeletons have long attracted biological interest and have provided the main taxonomic characteristics used to classify radiolaria. In general, taxonomic criteria distinguishing species have included the overall shape of the skeleton, whether spherical, spiral, oval, or occurring as scattered spicules, etc. Further distinctions have been made on the number of concentric hollow spheres in the skeleton, or the geometry and arrangement of pores. Number and arrangement of surface spicules and spines also have been used widely in making taxonomic discriminations. The extensive use of skeletons as taxonomic indicators may be attributed to their elegant, geometric regularity and abundance in the sedimentary record (*e.g.,* Haeckel, 1887; Riedel, 1971). However, some species lack siliceous deposits or produce only few or scattered spicules in their peripheral cytoplasm making cytoplasmic morphology more significant in their taxonomy. Application of light and electron microscopic analyses of radiolarian cytoplasm has clearly contributed to finer taxonomic distinctions (*e.g.,* Hollande and Enjumet, 1953; Cachon and Cachon, 1977, 1985; Anderson, 1976, 1978a, b, 1983). The larger species producing little or no siliceous deposits have recently been investigated more extensively for their physiological and fine structural characteristics toward a more exact understanding

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of their functional morphology and phylogenetic affinities (*e.g.,* Cachon and Cachon, 1977; Anderson, 1978*a*, 1983; Swanberg and Harbison, 1980; Swanberg and Anderson, 1981; Anderson and Botfield, 1983). Some of these gelatinous, larger radiolaria reach diameters of several millimeters (Fig. 1), and are easily observed with the unaided eye and appear as opalescent, pale-green, or yellowish spheroidal bodies suspended in seawater.

Among these larger, gelatinous, solitary species of radiolaria, Haeckel (1887) described ten genera and forty-two species. The major diagnostic generic features he used were the presence or absence of alveoli within the large central capsule or in the peripheral envelope of cytoplasm known as the extracapsulum, and the occurrence and form of spicules in the extracapsulum. Of these species, *Physematium atlanticum* (Meyen, 1834) was one of the earliest of radiolaria identified. We have found this organism in great abundance near Barbados in December and January, and in the southern Sargasso Sea especially during the months of February and March, where it is often the commonest large solitary spumellarian in the surface waters. Unfortunately, the original description is rather ambiguous. Schneider's description (1858) of *P. muelleri* is unambiguous, however, and as it has priority over Haeckel's taxa, we have assigned our material to this species.

P. muelleri is characterized by a large, somewhat opalescent, spheroidal cell body (1–5 mm dia.) surrounded by a hyaline gelatinous layer making the total diameter of the organism 3–6 mm. Fine axopodia radiate peripherally through this gelatinous sheath. The nucleus was described by Haeckel as possessing a thick membrane surrounded by an alveolate intracapsulum with a thin capsular wall, though Cachon and Cachon (1977) have shown that the intracapsulum is not alveolate, based on fine structure evidence. The presence of C- or S-shaped, siliceous spicules in the extracapsulum distinguish *P. muelleri* from its close relative *Thalassolampe margarodes* based on the classical description. Brandt (1902) maintained that the presence of such isolated siliceous spicules were of limited systematic use at higher taxonomic categories, and then only when the soft body parts could be considered to be definitively different. He revised Haeckel's systematic scheme to place these genera together in the family Physematidae. He further observed that the cytoplasmic structure of *Physematium muelleri* and *Thalassolampe margarodes* agreed so closely as to make the latter genus superfluous; hence he recommended that the skeletonless genera be grouped with the older established genus *Physematium.* Modern researchers (Hollande and Enjumet, 1953; Cachon and Cachon, 1977; 1985) have accepted Brandt's familial designation but followed Haeckel's scheme in retaining the genus *Thalassolampe* for non-spiculate organisms.

Although the spicules constitute a salient feature for systematic categorization, potentially, one of the most biologically significant characteristics of *Physematium* is the organization of the cytoplasm into a large gelatinous, spheroidal form with intracapsular lobes. These lobes vary in arrangement from a loosely packed anastomosing network with large peripheral vacuoles (as in *Physematium*) to more closely spaced lobes with numerous small peripheral vacuoles near the capsular wall (as in *Actissa*). The functional significance of this organization is examined in relation to host-algal symbiotic associations, prey apprehension, buoyancy functions, and possible phyletic relationships among related genera. To further elucidate the contribution of spicule number and morphology to the systematics of these large, gelatinous solitary radiolaria, we have examined the variation in spicule abundance and morphology in specimens collected by divers in open ocean locations near Barbados and in the Atlantic Ocean.

Materials and Methods

Individual organisms were collected into hand-held glass jars by divers in the Caribbean Sea at a location approximately 1 mile from the west coast of Barbados, West Indies, during the month of January and at open ocean locations near Bermuda in the months of May and June, or during collection at sea in the North Atlantic Ocean (research cruises, OCEANUS 115 and 170, KNORR 53 and 94, ISELIN 83-1, and 83-11, CALANUS 85-5, and JOHNSON SEA-LINK). Specimens collected near Barbados were fixed for electron microscopy (Anderson, 1976), embedded in epoxy (LX 112), sectioned with a diamond knife, and ultrathin sections collected on uncoated copper grids. Sections were post-stained with Reynold's lead citrate and observed with a Philips EM 200 or EM 201 electron microscope operated at 60 kV. Other specimens were fixed immediately after capture using cacodylate-buffered 3% glutaraldehyde (pH = 7.8) and refrigerated for later examination by light microscopy and preparation for scanning electron microscopy. Specimens for scanning electron microscopic examination were rinsed in distilled water, immersed in 10% v/v ethanol to prevent large ice crystal formation during freezing, deposited on scanning microscope stubs, frozen in liquid nitrogen, and freeze-dried under vacuum. A Cambridge Stereoscan 250 Mk2 scanning electron microscope was used to examine the specimens.

Results

Light-microscopic views of the whole organism (Fig. 1) exhibit the large centrally located nucleus, widely spaced lobes, and alveolate intracapsulum, enclosed by a thin capsular wall adorned with a thin layer of loose spicules (Fig. 2) of varying morphology but typically appearing as C- or S-shaped structures (*ca.* 100–150 μm in length). An overview of the organization of the central capsule is presented in the composite line drawing (Fig. 3) and low-magnification electron microscopic perspective (Fig. 4). The organization and position of the nucleus (N), the surrounding radially arranged lobes and their relationship to the thin peripheral capsular wall (CW) is illustrated in Figures 4 and 5. Numerous cytoplasmic strands (fusules) occur in the capsular wall and connect the intracapsular cytoplasm with the radiating rhizopodia penetrating the peripheral jelly layer. The intracapsular lobes are widely spaced and interconnected by thin strands of cytoplasm. Alveoli formed by large vacuoles surrounded by a thin layer of cytoplasm within the intracapsular lobes occur sporadically within the central capsular cytoplasm and more commonly at the perimeter near the capsular wall. Higher magnifications of the nucleus (Figs. 6, 7) exhibit the perinuclear perforated organic wall and extensions of the nucleus through the pores into the surrounding cytoplasmic lobes. The perinuclear organic wall exhibits a finely fibrous texture and is enclosed within a cisterna produced by cytoplasmic extensions of the intracapsular lobes (Arrow, Fig. 7). The nuclear membranous envelope is separate from the cisternal membrane enclosing the fibrous matter of the perinuclear wall and exhibits a structure typical for eukarayotic cells with transmembranous pores. The intracapsular lobes are richly supplied with mitochondria, Golgi bodies (Fig. 8), and electron-dense granules, frequently grouped with peroxisomes in clusters (Fig. 9). Groups of mitochondria are commonly observed encircling a cluster of electron-dense granules and smaller mitochondria (arrow, Fig. 4). Occasional peroxisomes are distributed at the periphery of the ring of mitochondria, and some of the peroxisomes encircle the mitochondria (Fig. 9) indicating a close structural and perhaps functional association. Large, less densely stained lipid droplets

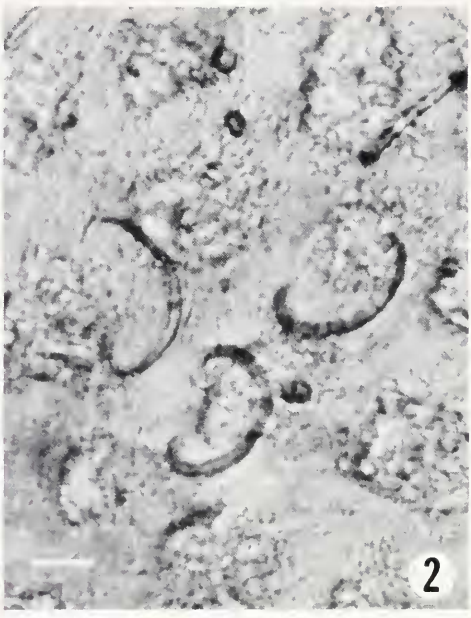


FIGURE 1. A living *Physematium muelleri* with prominent intracapsular lobes and a centrally located nucleus. Bar = 1 mm.

FIGURE 2. Siliceous spicules on the surface of the central capsular wall of *P. muelleri.* Bar = 20 μm.

are also observed in the regions of the cytoplasmic lobes where the ensembles of encircling mitochondria and dense granules are abundant.

The capsular wall possesses numerous fusules (strands of cytoplasm) directed outward, forming continuity between the intracapsular lobes and the extracapsular rhizopodial assembly (Fig. 5). The fusule structure resembles that in other large species of solitary radiolaria (*e.g.,* Anderson, 1976, 1983, p. 114), consisting of a thin strand of cytoplasm emerging from a tip of an intracapsular lobe, penetrating the capsular wall to which it is attached, and emerging on the extracapsular side as an electron-dense segment surrounded by a collar-like rim. The rim is perforated by micropores, giving a sieve-like quality to the wall of the rim. Distal portions of the extracapsulum exhibit rhizopodia and digestive vacuoles of varying diameter. Scanning electron microscopic views of the surface of the central capsule (Figs. 10, 11) show that the fusules occur in small clusters distributed over the surface of the central capsule. This is consistent with the transmission electron microscopic evidence showing long spaces of capsular membrane separating groups of fusules.

As a contribution to the comparative fine structure of *Physematium* and its relatives, we have examined the capsular organization of *Actissa* sp. collected at the same location near Barbados (Fig. 12). The peripheral capsular cytoplasm is more dense than that of *Physematium,* and possesses large peripheral vacuoles near the capsular wall as described earlier by light microscopic investigations (*e.g.,* Haeckel, 1887). These fine structural data confirm one of the distinguishing characteristics of the two species reported by Haeckel, *i.e.,* the presence of a thickened organic wall and large intracapsular spheroidal vacuoles in *Actissa,* and their absence in *Physematium.* Prominent outward directed collars (asterisk, Fig. 12) in the capsular wall of *Actissa* enclose the

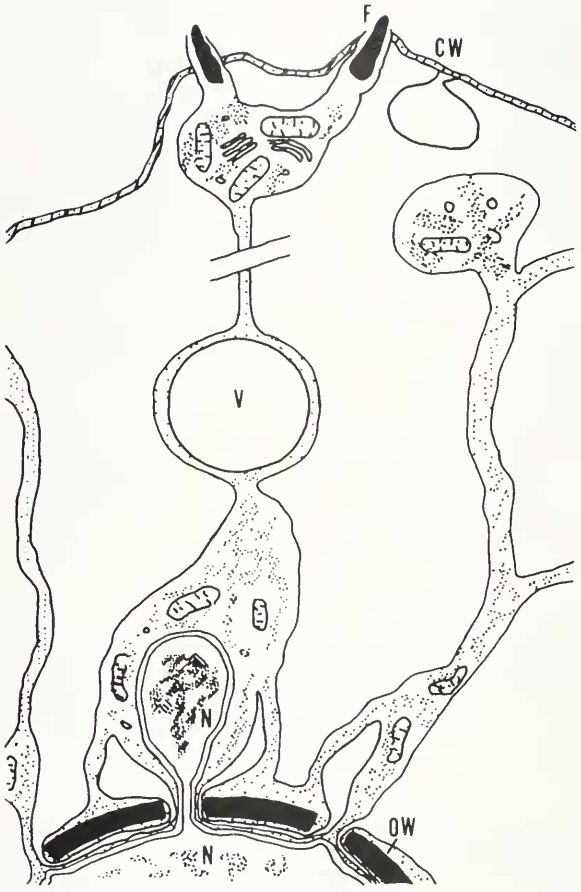


FIGURE 3. A line drawing illustrating a segment of the central capsular cytoplasm including the nucleus (N) with a thick organic wall (OW), radially arranged, widely spaced lobes with large vacuoles (V), and a thin peripheral capsular wall (CW) bearing the fusules (F) connecting the intracapsulum with extracapsulum.

fusule cytoplasmic strands. Numerous mitochondria and occasional segments of endoplasmic reticulum occur in the region proximal to the vacuolar layer.

Symbiont fine structure

We have observed very small yellow-green to yellow-brown symbionts (*ca.* 3–4 μm dia.), similar to those figured by Hollande and Enjumet (1953), in the extracapsular cytoplasm of both *Physematium* and *Actissa*. The fine structure of the symbionts (Fig. 13) indicates they are one of the Chrysophycophyta (eukaryotic yellow-green pigmented flagellates) with plastids composed of lamina with three thylakoids. The double membrane of the nuclear envelope encloses the plastids which are found occasionally in a parietal position within the cytoplasm. A granular pyrenoid within the plastid is penetrated by thylakoid membranes (Py, Fig. 13) and is prominently displayed in longitudinal sections. Mitochondrial lobes with tubular cristae and profiles of Golgi bodies

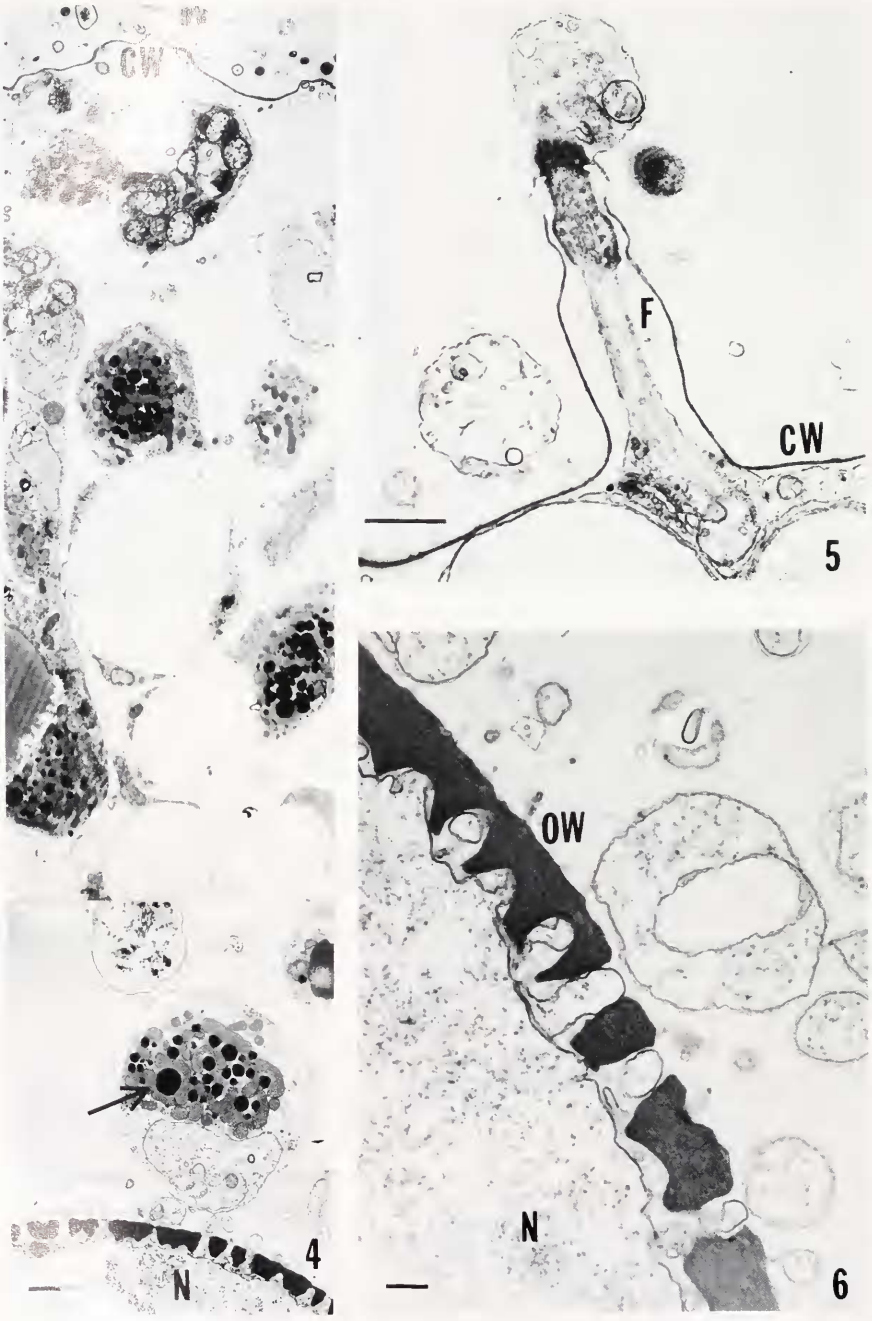


FIGURE 4. A montage of representative transmission electron microscopic sections along a radial dimension from the nucleus (N) to the capsular wall (CW) exhibits the thick, porous, nuclear wall, surrounding cytoplasmic lobes, and the peripheral thin capsular wall. Clusters of densely stained lipid deposits and mitochondria (arrow) occur abundantly in the intracapsular lobes. Bar = 5 μm.

FIGURE 5. Fusule detail showing the protrusion of the capsular wall (CW) surrounding the cytoplasmic strand (F) projecting distally from the central capsule. Bar = 1 μm.

FIGURE 6. An enlarged view of the thickened wall (OW) surrounding the nucleus (N) with lobate projections of the nucleus in the pores and extending into the perinuclear space. Bar = 1 μm.

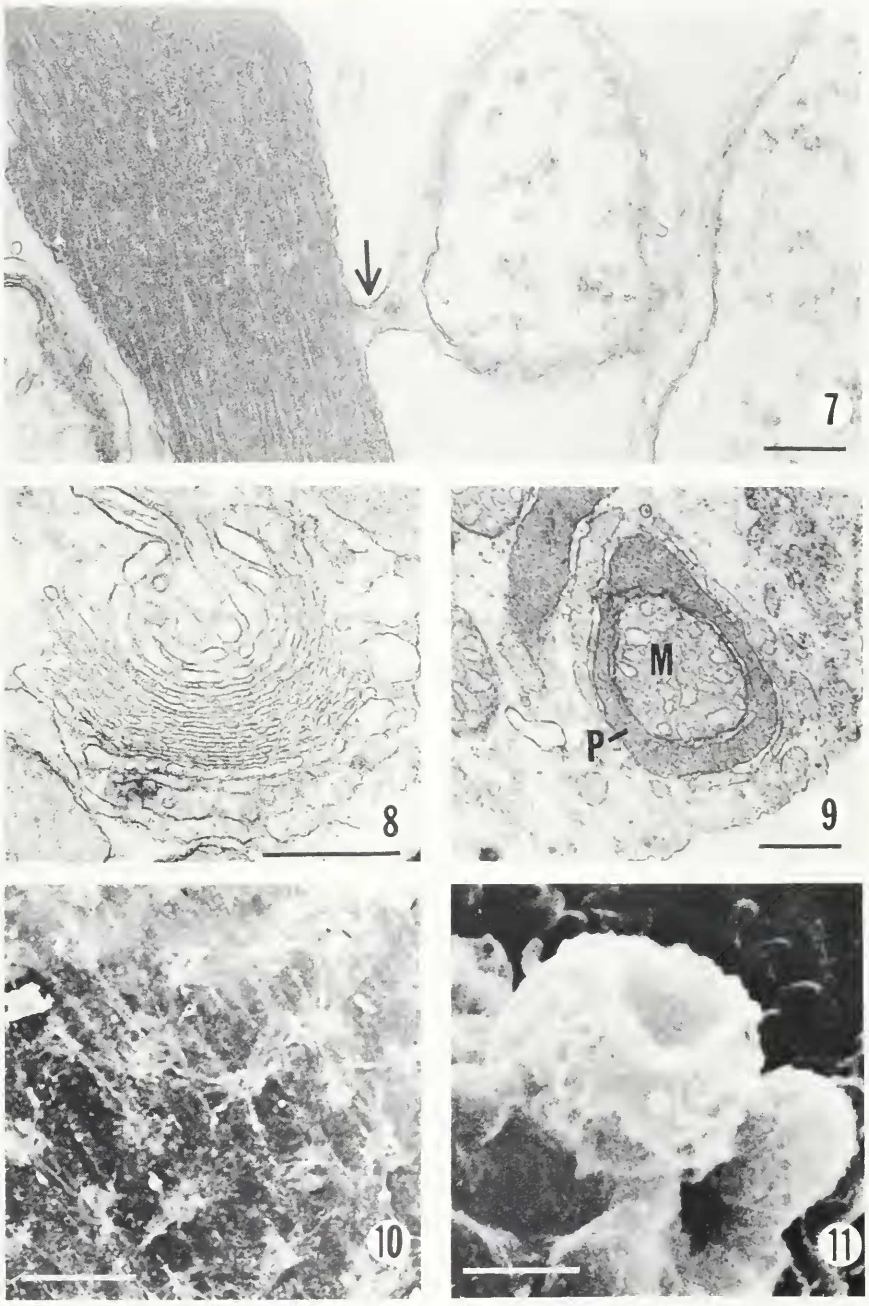


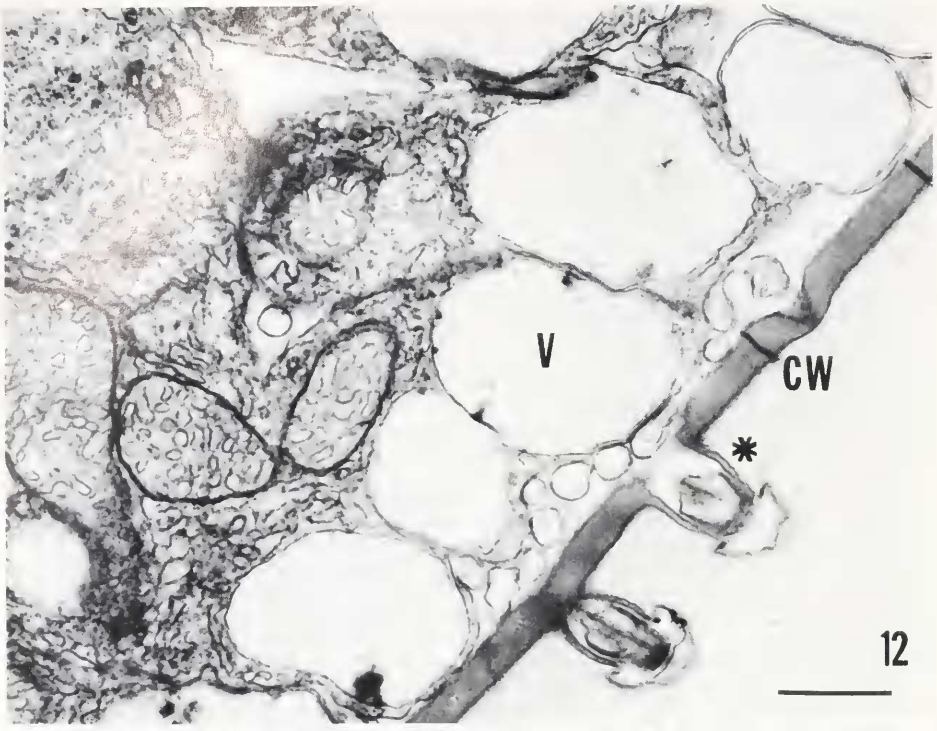
FIGURE 7. A detailed view of the organic wall surrounding the nucleus, showing the fine fibrillar quality of the organic substance in the wall and the enclosing living membrane (arrow) extending from a nearby cytoplasmic lobe. Bar = 0.5 μm.

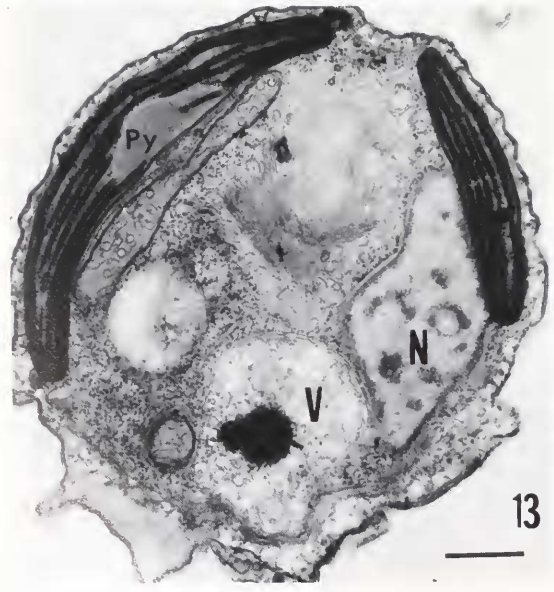
FIGURE 8. Golgi apparatus in a segment of an intracapsular lobe of *Physematium muelleri*. Bar = 0.5 μm.

FIGURE 9. A close spatial association occurs frequently between mitochondria (M) and peroxisomes (P) which sometimes encircle the mitochondria. Bar = 0.5 μm.

FIGURE 10. A scanning electron microscopic view of the surface of the central capsular wall showing the arrangement of fusules. Bar = 50 μm.

FIGURE 11. A higher magnification view of a fusule and surrounding rhizopodia on the central capsular wall. Bar = 1 μm.





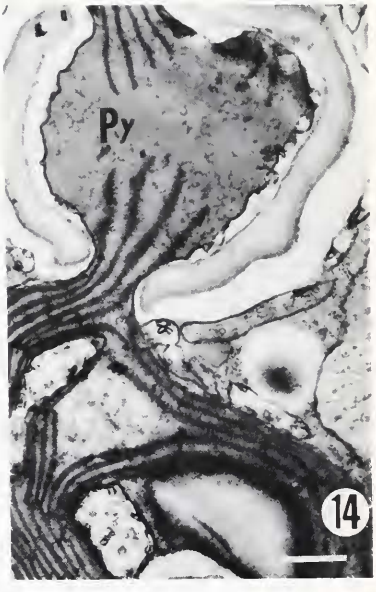


FIGURE 12. The peripheral intracapsular organization in *Actissa* sp. exhibits the large peripheral vacuoles (V) in the cytoplasm and thickened capsular wall (CW) with short fusules (asterisk) directed peripherally. Bar = 1 μm.

FIGURE 13. A section of a yellow-green pigmented algal symbiont (*ca.* 3 μm diameter) associated with *Physematium muelleri* and *Actissa* sp. The parietal plastids with internal pyrenoids (Py) are enclosed within the double membranes surrounding the nucleus (N). Storage vacuoles (V) are commonly observed in the symbionts. Bar = 0.5 μm.

FIGURE 14. The fine structure of the pyrenoid (Py) and its surrounding starch sheath within a dinoflagellate symbiont associated with *P. muelleri*. Bar = 0.5 μm.

are scattered throughout the central cytoplasm. Some symbionts possess a large excentrically located vacuole which is electron luscent or sometimes contains amorphous matter or densely staining granules (V, Fig. 13). We have not observed flagella, probably owing to the coccoid state of the algal cells as is typically observed in a symbiotic association with radiolaria (*e.g.,* Anderson, 1976, 1983; Anderson *et al.,* 1983). *Physematium* sp. also possess dinoflagellate symbionts (Fig. 14) resembling those previously observed in radiolaria (Anderson, 1976, 1983). In some cells, we have observed as many as three pyrenoids, while in previous observations of dinoflagellate symbionts (identified as *Amphidinium* sp.) there were either one or two pyrenoids.

Spicule abundance and morphological diversity

A sample of 60 specimens exhibiting a gross morphology of *Physematium* was examined to determine the abundance of spicules within the cytoplasm immediately surrounding the central capsular membrane. The abundance varied from no spicules to a few to hundreds and thousands per organism, suggesting an intergradation in spicule density among specimens. We suspect that spicule number may not be a good characteristic to distinguish species and therefore suggest that additional research is needed to evaluate Haeckel's assumption that spicule presence or absence is a species-specific trait. The absence of spicules may be due to a physiological state of the organism, rather than a genetic difference. A survey of 121 specimens of SCUBA-collected *Physematium muelleri* was made to determine the morphology of the spicules. The shape of the spicules was categorized as (1) straight needles, (2) C-shaped, (3) mixture of C-shaped and S-shaped, (4) mixture of C-shaped and straight, or (5) a mixture of shapes including all of the above and C-shaped forms with a small side branch. Fifty-four had simple straight spicules, 34 had C-shaped spicules, 5 had a mixture of C-shaped and S-shaped, 14 had a mixture of straight and C-shaped, and 14 had a mixture of heterogeneous shapes mentioned above. These data indicate that gradations in mixtures of spicule shape occur in specimens collected from the same locality, and that spicule type is probably not a good criterion for erecting separate species. The general intergradation of form of the spicules also exemplifies the remarkable heteromorphic variability in spicule composition of Radiolaria and raises the more general issue of the merit of using fine skeletal details in setting species boundaries.

Discussion

There is a component of arbitrariness inherent in all taxonomic criteria and the hierarchy of relative importance of various features is inescapably anthropocentric; this is particularly predominant in the systematics of radiolaria because of the salient aesthetic properties of their cytoplasmic and skeletal morphology. In recent publications, we have partially addressed the issue of taxonomic criteria and the appropriate kinds of attributes that may be most productive in developing a phylogenetically sound and heuristically valid taxonomic paradigm (Anderson, 1983, pp. 82–84; Swanberg and Anderson, 1985; Swanberg *et al.,* 1985, 1986). Our research on solitary and colonial radiolarian physiology (*e.g.,* Anderson, 1978b; Anderson and Botfield, 1983; Swanberg, 1983; Anderson *et al.,* 1985; Swanberg and Anderson, 1985) of *Spongodrymus* sp. and related spongiose skeletal solitary Spumellaria has given us an opportunity to examine in some detail a number of the larger, gelatinous Spumellaria including *Actissa, Physematium, Thalassolampe,* and *Thalassicolla.* A summary of our current understanding of the major morphological and fine structural features distinguishing these four genera is presented in Table I.

TABLE I

Major taxonomic characteristics of some larger gelatinous radiolarian genera

Taxonomic attribute	*Actissa*	*Physematium*[1]	*Thalassolampe*[1]	*Thalassolampe*
Cell dia. (mm)	0.2–1.5	1.0–12.0	2–15	1–6
Central capsule dia. (mm)	0.1–0.2	1.0–10.0	2–12	0.1–2.5
Cytoplasmic organization				
Nucleus	spherical, envelope thin, composed of double membrane	spherical, enclosed within thick organic wall within nuclear envelope	spherical, enclosed within thick organic wall within nuclear envelope	spherical, envelope thin membranous
Intracapsular lobes	closely grouped but with peripheral vacuoles near the capsular wall	forming a network of strands with fluid-filled, alveolate spaces	alveolate and widely spaced radial lobes	closely spaced radial lobes, dense cytoplasm
Capsular wall	thin organic wall within membranous envelope	thin, membranous, with organic deposit in cisterna	thin, membranous, with organic deposit in cisterna	thick organic wall in cisterna of capsular membrane
Extracpsular organization	thin, non-alveolate	thin, non-alveolate	thin, non-alveolate	robust, alveolate forming frothy cytoplasmic layer
Siliceous deposits	none	spicules few to many, of varied shape (S, or C-shaped)	none	none

[1] Note: See text, although these are separated in previous treatments, our data suggest these two genera may be merged.

Our evaluation of the fine structure of the cytoplasm of these organisms in relation to skeletal spicule variation has been informed by the observations of Hollande and Enjumet (1960, p. 66) decrying the poor systematic value of some skeletal variations, especially the significance of lattice versus spongiose skeletal morphology, and has led us to re-evaluate the importance of spicule abundance and morphology in erecting generic categories. This critical re-appraisal seems especially relevant to *P. muelleri* because of its unusual delicate spicules and the unique features of its large spheroidal central capsule including the very thin capsular membrane and the substantial perinuclear wall. We consider these features to be significant phyletically and taxonomically and representative of a functional morphology adapted to enhance buoyancy, algal symbiont associations, and possibly prey apprehension.

We present the first observation of a yellow-green pigmented chrysophyte-type alga in association with radiolaria. It is not immediately clear, however, why some individuals possess the yellow-green pigmented algal associates while others have dinoflagellate symbionts. Similar thin-walled cytoplasmic sheaths of host cytoplasm surround both kinds of algae, but we do not know if the physiology of the association, including kind and translocation rate of photosynthates from alga to host, is similar for the two types of algae.

The cytoplasmic organization of the larger gelatinous Spumellaria suggests a phylogenetic pattern of development progressing from an ancestral form resembling *Physematium* with a thick perinuclear wall and delicate vacuolated capsular cytoplasm toward *Actissa* with a thickened capsular wall, rather closely packed cytoplasmic lobes bearing numerous peripheral alveolate vacuoles, but still lacking extracapsular alveoli. At a more advanced stage, an organization more characteristic of modern *Thalassicolla* sp. may have emerged, with densely packed intracapsular lobes of cytoplasm, a thickened porous capsular wall, and a massive array of extracapsular alveoli.

Our fine structural analyses of *P. muelleri* show that the delicate intracapsular cytoplasm supporting the thin central capsular membrane provides a large increase in cell volume with moderate cytoplasmic elaboration. This delicate construction, while increasing surface area and conserving cytoplasmic mass, also leaves the nucleus relatively unprotected. The thickened perinuclear wall may provide protection for the nucleus suspended within the delicate web of anastomosing intracapsular lobes. The adaptive value of the radially arranged lobes with large intra-lobular spaces is not obvious. Observations of living specimens floating in the open ocean and in laboratory culture indicate that, like many gelatinous Spumellaria, these organisms are neutrally buoyant. This buoyancy may be attained by secretion of low density fluids within the free space among the lobes. The presence of a fluid within the central capsule has been confirmed by piercing the organisms in laboratory culture. In most cases, the pierced organisms exude the fluid, but do not burst. The capsular membrane eventually heals and the large inflated form is re-established.

The functional morphological significance of these features appears to be profound. An hypothetical spherical organism relying on density-dependent predation for food is under selective pressure to increase its ratio of surface area to volume with minimum expenditure of energy and maximum utilization of cytoplasmic mass (Anderson, 1985, Swanberg *et al.*, 1985). One way to accomplish this is to protrude thin lobes of cytoplasm either supported on delicate, elongate skeletal elements if present (Anderson, 1983, pp. 178–180, 1985; Swanberg *et al.*, 1985) or attached to a thin lamina such as the delicate capsular membrane to increase the associative strength while simultaneously keeping the amount of supporting surface cytoplasm at a minimum. Few skeletonless organisms appear to have employed this option as observed in *P. muelleri*. A large surface area for improved symbiont holding capacity and greater probability of prey

apprehension, is produced while the large fluid-filled spaces between the delicate cytoplasmic lobes provide volume at low metabolic expense. Although the capsule contour remains spherical, the total cytoplasmic surface area is large relative to the smaller, metabolically active volume. The radiating delicate axopodia surrounding the globose central capsule are efficiently disposed to provide a large prey apprehending area.

Haeckel considered *Actissa* to be the most "primitive" of the radiolaria. Our observations suggest that in its ultrastructure *Physematium muelleri* is actually closer to a simple spherical cell and more primitive in its organization of the capsular cytoplasm than many Spumellaria. The adaptation to increased surface area at low metabolic cost is a major strategy for a number of groups of gelatinous metazoan predators such as Coelenterata and Ctenophora in the open ocean. If, indeed, *Physematium* is a primitive form of radiolarian, the evolution of a light-weight, large-surface-area morphology may have been an early adaptation that preceded massive skeletal deposition as a means of supporting and enhancing large cytoplasmic surfaces in these symbiont-bearing, opportunistic planktonic predators.

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